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The vegetation of Connecticut

IV. Plant societies in lowlands*

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(WITH FIFTEEN TEXT FIGURES)

The term LOWLAND, as used in the present paper, embraces primarily lakes, ponds, and swamps.† The word LAKE may be employed to designate any body of water surrounded by land, but more commonly this term is applied to relatively large bodies of water, smaller water bodies being referred to as PONDS. Throughout the present paper the two terms are used more or less indiscriminately. A SWAMP may be defined as any area where the ground is saturated with water throughout a good part of the year, but where, at least during most of the year, surface water does not accumulate. As will be seen presently, it is not always possible to differentiate absolutely between lakes and ponds on the one hand and swamps on the other. Thus, the transition from a lake to the swamp at its margin may be so gradual that one cannot say where the one leaves off and the other begins. Similarly, a swamp may merge by almost imperceptible gradations with the neighboring upland, so that it is likewise difficult to draw a sharp line of demarcation between lowlands and uplands.

* Contribution from the Osborn Botanical Laboratory. The previous numbers of this series have appeared in Torreya **13**: 89–112; 199–215. 1913, and **14**: 167–194. 1914. In this paper, as in the others, the nomenclature followed is that of Gray's Manual, seventh edition.

† In earlier papers this term has also been used to designate one of the three geographic provinces into which the state is divided, viz., Central Lowland, as contrasted with Eastern and Western Highlands.

[The BULLETIN for March (**42**: 93–168. *pl. 9*) was issued March 16, 1915.]

GEOLOGICAL RELATIONS OF LAKES AND SWAMPS

The Effect of Physiographic Factors on the Distribution of Lakes and Swamps.—In a general way it can be said that lakes and swamps belong to the same family, and differ only in age.* Lakes, however, "are temporary features of a landscape, and can only exist where the land has been recently raised above the sea or modified by some widely acting agent"† such as glaciers. Sooner or later they are destined either to be drained through the activity of streams cutting down their outlets, or else to be filled in through the washing in of inorganic sediment from without and the accumulation of vegetable debris from within.

Considered from the standpoint of their physiographic origin, Connecticut lakes may be grouped under three heads: GLACIAL, RIVER, and COASTAL. The term GLACIAL LAKE is here used in its broadest sense, to include lakes formed in any sort of a depression resulting from glacial activity. Glacial lakes may further be subdivided as follows: (1) MORAINAL LAKES—those associated with accumulated glacial debris of any description; and (2) SCOOP LAKES—those which occupy depressions scoured out of the underlying rock by the ice. Lake Saltonstall, near New Haven, affords a striking example of a scoop lake. This lake is about three miles long and has an extreme depth of 108 feet, more than eighty feet below sea level; yet notwithstanding that the tides rise and fall at its very edge, its water is fresh and constitutes part of the New Haven water supply.‡ On the whole, however, scoop lakes are far less abundant and of much less importance in Connecticut than morainal lakes, and of the 1,026 lakes indicated on the topographic map of the state§ the great majority belong to this latter class. Morainal lakes may originate under a variety of conditions. Thus, (*a*) they may occupy depressions in the ground moraine; (*b*) they may occur behind dams formed by the heaping up of glacial till; (*c*) they may occupy depressions in stratified drift; or (*d*) they may develop behind the ridges of stratified drift known as eskers. Morainal lakes of the first two types here mentioned

* Possible exceptions to this statement are pointed out in later paragraphs.

† Rice, W. N., and Gregory, H. E. Manual of the geology of Connecticut, Geol. and Nat. Hist. Surv. Connecticut, Bull. 6: 248. 1906.

‡ See Rice and Gregory, *op. cit.*, p. 249.

§ See Rice and Gregory, *op. cit.*, p. 247.

are common throughout the state, but are especially characteristic of the higher, more rugged sections. Morainal lakes of the last two types are best developed in the lower, leveler, central portion of the state. Lakes occupying depressions in stratified drift are well exemplified by the "kettle-hole" ponds, so abundant in the sand-plains near New Haven; while Lake Compounce is a good illustration of a lake dammed in by an esker.

RIVER LAKES or PONDS for the most part are associated with old-age, meandering streams. In general, they are of two sorts: (1) OX-BOW and (2) MARGINAL. Ox-bow ponds, originating in flood time as a result of the abandonment of old water courses, are common along sluggish streams throughout the state (FIG. 1).

FIG. 1. Ox-bow swamp along Muddy River, North Haven. In the foreground are seen *Castalia odorata* (in the water), *Dulichium arundinaceum* (along the left bank), tufts of *Carex stricta* (on both banks). Elm, etc., in the background.

Marginal ponds are often caused by the deposition of sediment along the bank of a stream at high water, thereby gradually building up a sort of dike or ridge which cuts off the channel from

the remoter parts of its flood plain. When the stream overflows its banks these latter areas are flooded, and after the recession of the water there may be left behind more or less extensive shallow ponds. Such ponds may be seen along the Connecticut River and elsewhere, but usually they are of a very temporary nature. Far more common than marginal ponds are marginal swamps. These may originate in the manner just described, but more often seepage water is responsible in large measure for the maintenance of the swampy condition. Swamps due to seepage will be discussed presently.

COASTAL LAKES, PONDS, and SWAMPS are formed mainly behind barrier beaches, in sheltered bays and harbors, and along the lower courses of the larger rivers. The ecological relations of these will be considered in a later paper, in connection with plant societies along the coast.

The Effect of Topography and Ground Water Level on the Character of Lakes, Ponds, and Swamps.—It is evident that topography, as moulded by physiographic forces, is an all-important factor in governing the distribution of lakes and ponds. This is also true with respect to swamps, but it is further true, as will be pointed out presently, that swamps may be developed in areas where bodies of standing water could not exist. Yet while their development is dependent on suitable topographic conditions, the presence or absence of lakes, ponds, and swamps is further conditioned by the relation between the level of the land surface and the water table; and this in turn is influenced by the amount of precipitation and the character of the substratum. The surface of the ground water rises and falls with the land surface, but with smaller differences of elevation. Thus, while it reaches its highest elevation in the hills it stands farthest from the surface of the ground there. Similarly, in the depressions it stands lower, but is nearer the surface of the ground. Wherever it reaches the surface, lakes, ponds, streams, or swamps may be formed.* Owing to the variation in the amount of precipitation at different seasons of the year, the level of the water table is constantly

* For an extended discussion of the underground water resources of Connecticut, see Gregory, H. E., and Ellis, E. E., U. S. G. S. Water-Supply Paper 232, pp. 1–200, *pls. 1–5 + figs. 1–31.* 1909.

fluctuating. It is highest during winter and spring, the seasons of maximum precipitation; it is lowest in late summer, toward the end of the season of minimum precipitation. In the following paragraph, the writer has attempted to bring out, with the help of diagrams (FIG. 2), the important bearing which these various factors may have on the nature of lakes, ponds, and swamps.

With reference to their relation to topography and water table, four fairly distinct types of lowland may be recognized. (1) PERMANENT LAKES OR PONDS.—Where the relationship between the controlling factors, i. e. topography and water table, is such that a tract of land is submerged to an appreciable depth by standing water throughout the year (FIG. 2, A), it is obvious that a permanent lake or pond will exist. It need hardly be remarked that such a water body can arise only within a completely enclosed basin. Lakes fed entirely by subterranean waters are not uncommon, but more frequently this source of supply is supplemented by surface streams. A permanent water body can exist in a closed basin only where the amount of water flowing in exceeds the amount lost through underground drainage plus the amount lost through evaporation. (2) INTERMITTENT LAKES OR PONDS.—Very often the relationship between the various factors involved is such that a basin is filled with water in spring, but later in the season, as a result of the lowering of the water table plus increased evaporation, the surface water vanishes, leaving the bottom of the depression quite dry, or else merely swampy (FIG. 2, B). Shallow, intermittent ponds of this sort are of frequent occurrence, being especially well developed in parts of the sand plains north of New Haven. (3) PERMANENT SWAMPS.—It often happens that, in spite of an abundant supply of underground water, topographic relations are such as to prevent pond formation. Thus, seepage water may keep the ground on a side hill wet throughout the year, but as fast as the water reaches the surface it runs off to lower levels. Similarly there may be a series of perennial springs along the base of a hill, but in the absence of an enclosed basin of some sort to contain the water, pond formation manifestly cannot take place, and swampy conditions prevail. Ideal conditions for permanent swamps are presented by the flat floors of the old glacial drainage valleys, so common throughout central Connecticut. Lying well

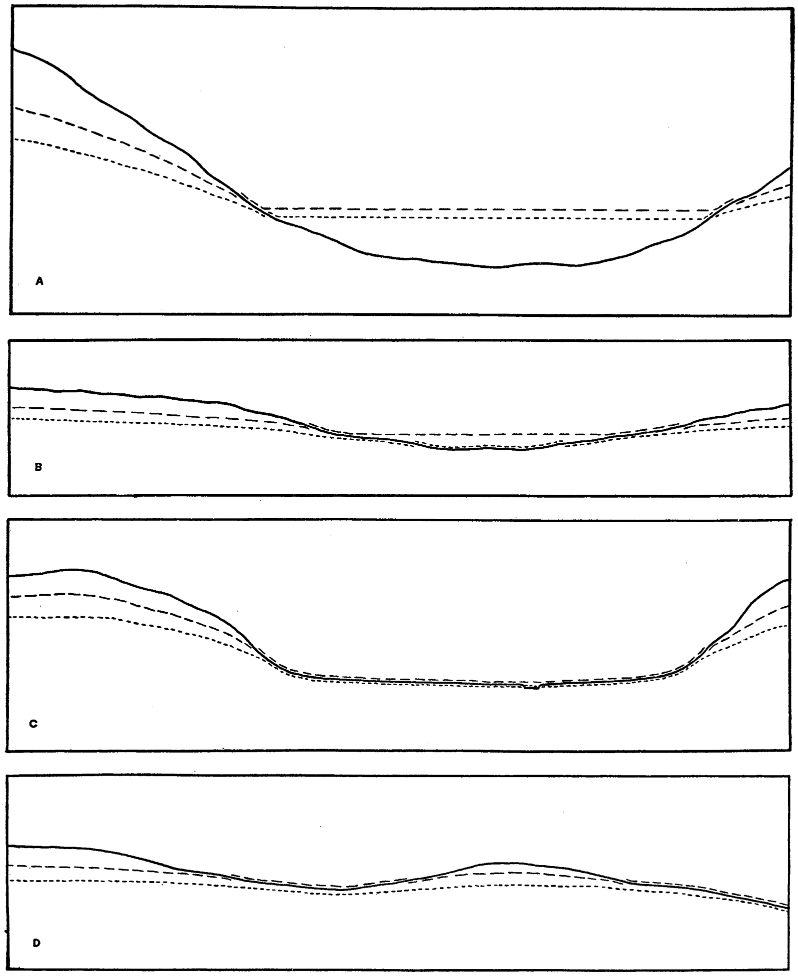

FIG. 2. Diagrammatic vertical sections to represent the relation of topography and level of ground water to character of lakes, ponds, and swamps. Surface of Ground represented by continuous line (———), Level of Ground Water in Spring by long dashes (– – – –), Level of Ground Water in Late Summer by short dashes (- - - - -). A. Permanent Lake or Pond. B. Intermittent Lake or Pond. C. Permanent Swamp; cross section of a glacial drainage valley. From this diagram the relations of topography and water table might at first thought appear identical with those represented by diagram A; but a longitudinal section would show this (C) depression to be in the nature of an open trough, rather than an enclosed basin (as in A). D. Periodic Swamp. For further discussion, see text.

below the general level of the water table at all seasons, as they usually do, the surface of the ground is kept constantly wet by springs and seepage water, but the surplus is continually being carried away by the small streams which drain these areas. A cross section of one of these glacial-drainage-valley swamps is shown by FIG. 2, C. (4) PERIODIC SWAMPS.—These bear much the same relationship to permanent swamps that intermittent ponds bear to permanent ponds. In other words, in an area where the relations between topography and ground water level are such as to preclude pond formation at any season of the year, but where the ground is saturated with water at certain seasons and dry at others, a periodic swamp may be said to exist. Swamps of this sort are common on every hand—in low grounds, in shallow depressions of any description (as in FIG. 2, D), and on side hills.

Between the four types of lake, pond, and swamp above described, all intergradations exist, so that it is not always easy to assign a given lowland area to a definite category. But while this classification is necessarily elastic, and while improvements can doubtless be suggested, the scheme here proposed, it is believed by the writer, will prove serviceable in the study of the vegetation of lowlands, not only in Connecticut but elsewhere as well.

THE RÔLE OF VEGETATION IN THE CONVERSION OF LAKES INTO SWAMPS

The important rôle commonly played by plants in the conversion of lakes into swamps has long been recognized, and the manner in which this transformation is brought about may appropriately be outlined at this point. When the plants in a lake die, their remains sink to the bottom where, because of insufficient oxidation, the vegetable debris is only partially decomposed. In this way there collects on the floor of the lake a layer of vegetable muck, or peat; and through the continued addition of fresh layers the deposit is gradually thickened and built upward. This constructive process may go on until ultimately the surface of the deposit reaches the level of the water, when the lake gives way to a swamp (see FIG. 3). But the rate at which the substratum is built up and the length of time which elapses before it reaches the water level varies greatly in different parts of a lake. As will

be shown presently, plants grow most luxuriantly in shallow water; they may be practically absent from the deeper areas. It follows, therefore, that the accumulation of muck or peat proceeds much more rapidly in shallow than in deep water—so much so, in fact, that the shoreward parts of a lake may have become completely filled in before any appreciable accumulation has taken place in the deeper areas. The filling in of deep lakes usually proceeds centripetally. This is due to the fact that the shoreward zones of vegetation, in consequence of their more vigorous growth, exhibit a tendency to push outward into deeper water. Where this tendency is pronounced, the shoal water zones may completely override the deeper water zones, at the same time causing the lakeward slope of the deposit to become much steeper.* The filling in of the deeper parts of a lake may also be effected to a varying degree by the accumulation of loose debris from the adjoining shallows or by the deposition of sediment in flood time, while various plankton forms may contribute in a small measure to the deposit. But as a rule, the encroachment of the shoal water vegetation is the most important agency in bringing about the filling in of the deeper parts of deep lakes. The most extreme development of this method of filling is seen in connection with floating mat formation (FIG. 10), the discussion of which is reserved for later paragraphs.

THE SUCCESSION OF PLANT SOCIETIES IN LAKES AND SWAMPS

Succession in Lakes.—Coincident with the upbuilding of the substratum through deposition of muck or peat, as outlined in the preceding paragraph, transformations occur in the character of the vegetation growing on the lake's bottom. For, as the depth of the water diminishes, it becomes possible for plants to develop which were unable to grow in the deeper water. And as these shallow water plants increase in number and abundance, they may crowd out and eventually replace the deeper water species. Thus there may follow one another a series of plant societies,†

* For a more detailed description of this process, see Davis, U. S. Dept. Interior, Bur. Mines, Bull. 16: 22, 23. 1911.

† The terms Plant Society and Plant Association, in the present series of papers, are used indiscriminately and in their broadest sense. Except in referring to the Climatic Formation, the use of the term Formation has been avoided.

each one of which, by helping to raise the bottom of the lake to a higher level, prepares the way for less hydrophytic societies, but at the same time, by so doing, brings about its own extermination.

It is a familiar fact that the plants which fringe the edges of so many lakes are commonly massed in more or less definite bands or zones that tend to be concentric with respect to the deeper parts of the lake. The floristic composition of these zones in any given lake is determined largely by the ecological requirements of the various species of plants which happen to be present, in relation to the depth and clearness of the water. In progressing from the deeper parts of a lake toward the shore (FIG. 3) the zones

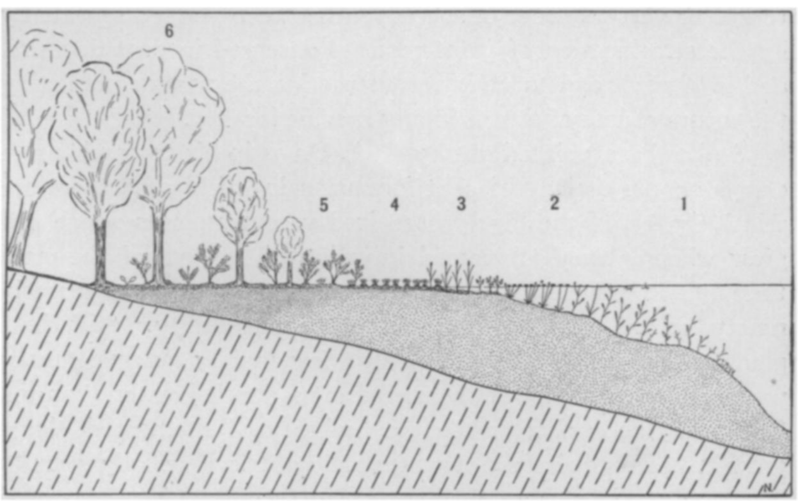

FIG. 3. Diagrammatic vertical section through the marginal portion of a shallow lake which is being filled in through the accumulation of vegetable debris on the bottom, showing the succession of plant societies which may accompany the transformation of a lake into a swamp. Sequence of Zones (or Stages): (1) Pondweed Zone; (2) Water-lily Zone; (3) Bulrush—Pickerel-weed—Cat-tail Zone; (4) Sedge Zone; (5) Shrub Zone; (6) Swamp Forest.

encountered, as characterized by the dominant plants, are usually: (1) the PONDWEED (*Potamogeton*) ZONE, (2) the WATER-LILY (*Castalia, Nymphaea*) ZONE, (3) the BULRUSH (*Scirpus*)—PICKEREL-WEED (*Pontederia*)—CAT-TAIL (*Typha*) ZONE (or ZONES), (4) the SEDGE (*Carex*, etc.) ZONE. Modifications of this arrangement are frequent, but in a general way the sequence is the same throughout the northern United States.

Reference has already been made to the succession of plant societies which accompanies the building up of the lake bottom. It has been found that this dynamic VERTICAL SUCCESSION corresponds closely with the apparently static HORIZONTAL ZONATION just outlined. Thus, in a hypothetical case, it may safely be assumed that the pondweeds now growing in a given locality are destined to be succeeded by water-lilies, the water-lilies by pickerel-weed, and these in turn by sedges. Conversely, sedges growing on a mucky shore have very likely been preceded by pickerel-weed, etc. This general coördination between the contemporaneous horizontal sequence of zones and the historical or vertical order of succession has been verified repeatedly by the stratification of plant remains observed in peat deposits, and is of great assistance in reconstructing the past or predicting the future course of events in any specific locality.

As has been pointed out by C. A. Davis in his comprehensive essays on the ecology of peat formation in Michigan,* there are relatively few of the highly organized vascular plants which can grow when entirely submerged in water. Thus, out of the more than 1,900 seed plants known to occur in Connecticut, scarcely ninety, or less than five per cent., have this ability. "Of these plants which will grow in water, only a few, mainly *Potamogetons* or pondweeds, can establish themselves at a depth greater than ten feet from the surface, while the majority of submerged plants grow in less than six feet of water, unless it is unusually clear."† The maximum depth at which seed plants can grow rarely exceeds fifteen to eighteen feet, so that the deeper parts of many lakes, owing to insufficient light, heat, and aeration, are practically destitute of vegetation. The first stage in the succession of plant associations which accompanies the filling in of a lake is the POND-WEED STAGE, characterized by the predominance of submersed aquatic plants, especially of species of *Potamogeton*. This genus is represented in Connecticut by no fewer than twenty-eight species, the commonest submersed forms of which are *P. Robbinsii*, *P. Richardsonii*, *P. pusillus*, *P. amplifolius*, and *P. heterophyllus*. The two species last named are capable of develop-

* Geol. Surv. Michigan 1906: 97–286. 1907.

† Davis, 1907, *loc. cit.*, p. 129.

ing two sorts of leaves, viz., submersed and floating; but the latter type is seldom formed on plants growing in water more than five feet deep. Flowers likewise are usually suppressed, except in shallow water, reproduction being accomplished solely by vegetative means. Other plants frequently present in considerable abundance in the pondweed association are *Najas flexilis*, *Vallisneria spiralis*, and *Elodea canadensis*. The lack of dependence of many of these water plants on the sexual methods of reproduction is well exemplified by the latter species. Introduced into Europe from America about 1836, this "Wasserpest" has become widely spread over that continent, notwithstanding that it has never been observed there in fruit. FIG. 4 shows a

FIG. 4. Submersed aquatics from Twin Lakes, Salisbury. The plants were placed on papers in the bottom of a boat and photographed fresh. Species shown are as follows: 1. *Potamogeton pectinatus;* 2. *P. lucens;* 3. *P. natans;* 4. *P. amplifolius;* 5. *P. heterophyllus;* 6. *Chara* sp.; 7. *Ceratophyllum demersum;* 8. *Elodea canadensis;* 9. *Sparganium minimum;* 10. *Eleocharis Robbinsii;* 11. *Utricularia intermedia;* 12. *Najas flexilis.*

representative collection of aquatic plants from a lake in northern Connecticut. The majority of such plants have roots and grow attached to the bottom, but there are a number of forms, notably

the bladderworts (species of *Utricularia*), *Ceratophyllum demersum*, and sometimes *Ranunculus aquatilis*, which are free floating and entirely unattached to the substratum. These usually grow near the surface and may be very abundant in sheltered coves. The pondweed zone, and the succeeding zones as well, may be broad

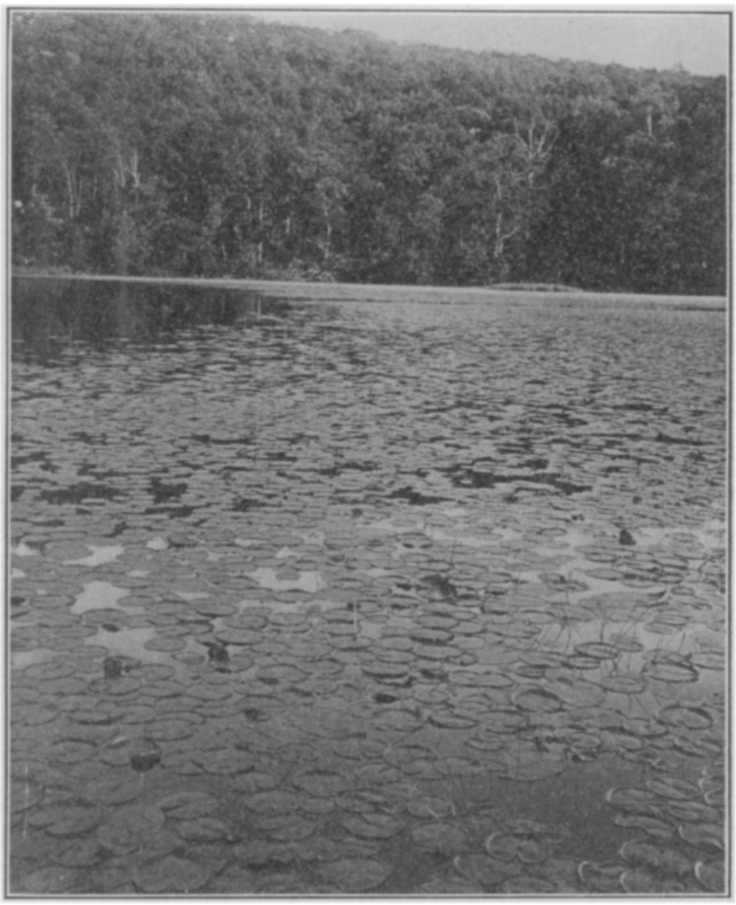

FIG. 5. Water-lilies (mostly *Castalia odorata*) at Round Pond, North Stonington.

or narrow, according as the bottom of the lake slopes gently or steeply.

In the absence of competition submersed aquatics develop best in shallow water, but as soon as the bottom has been raised high

enough, say within five or six feet of the surface, a higher order of plants—higher in an ecological sense—is able to develop, viz., plants whose leaves float upon the surface (FIG. 5). Most important among these are the water-lilies (*Castalia odorata* and *Nymphaea advena*), from the almost invariable presence of which this phase in the succession is called the WATER-LILY STAGE. As a rule the water-lilies come in with such force that they crowd out most of the submersed aquatics, for the shade produced by their large leaves is so great that nothing can live underneath them. One of the most remarkable structural peculiarities of the water-lilies is seen in their enormous rhizomes. These organs persist year after year, growing in length, sending out roots into the soft muck, and branching at intervals. In *Nymphaea advena* they

FIG. 6. Bulrushes (*Scirpus validus*) at Twin Lakes, Salisbury.

frequently acquire a length of fully eight feet, with a diameter of from two to three inches. When present in abundance they fulfil an important ecological rôle by holding together the loose deposits at the bottom of the lake. This same end is accomplished, though probably less efficiently, by the weak, slender roots and rhizomes of various submersed aquatics. Frequently other plants with floating leaves, such as *Brasenia Schreberi* and *Nymphoides lacunosum*, together with *Potamogeton epihydrus* and similar hetero-

phyllous pondweeds, grow in company with the water-lilies. The duckweeds (*Spirodela* and *Lemna*) and other free-floating forms also commonly occur here, but these, as might be expected, are not definitely restricted to any particular association.

With the continued shoaling of the water it becomes possible for plants to develop which root at the bottom and are partly submerged but whose foliage is raised above the surface of the water. As these increase in number, and as more and more light is intercepted by their aerial photosynthetic organs, species with floating leaves become scarcer and may be completely crowded out. This stage, because of the widespread prominence of the lake bulrush (*Scirpus validus*), the pickerel-weed (*Pontederia cordata*), and the cat-tail (*Typha latifolia*), may be referred to in a general way as the BULRUSH—PICKEREL-WEED—CAT-TAIL STAGE. But quite as often as not only one or at the most two of the character species will be conspicuous in a given lake or pond. Furthermore, where more than one is present, there is a marked tendency for one or another form to dominate locally. It would frequently seem as though the one first to arrive on the scene gained control. For these and other reasons it is convenient to divide this stage into the BULRUSH, the PICKEREL-WEED, and the CAT-TAIL SUBSTAGES. Roughly speaking, these three substages may be regarded as parallels. Thus in a given pond the pickerel-weed may fill the place occupied by the bulrush in another. Yet these substages cannot be regarded as absolute ecological equivalents. This is evidenced by the frequently observed zonal arrangement of the species concerned where two or three are present in the same pond. The cat-tail grows best in water only a few inches deep; the pickerel-weed thrives in water from six inches to nearly two feet deep; while the bulrush, although it develops best in shallow water, can grow in water more than five feet deep. Of the three species, the pickerel-weed (FIG. 7) is the most widely distributed and from an ecological standpoint the most important in Connecticut lakes and ponds. Scarcely a pond is encountered from which this plant is absent, and more often than not it forms a conspicuous fringe in the shoal water along the shore. The bulrush is abundant in many lakes, as at Twin Lakes, Salisbury (FIG. 6), but quite as often as not it is absent or else too poorly developed to be of any ecological significance. The cat-tails are

conspicuous marginal plants in some ponds, but on the whole cat-tail swamps are more characteristic of low flood plains along rivers than of pond margins. Very often a luxuriant development of cat-tails follows upon the removal of the original vegetation from a swampy tract by drought or some similar disaster. In

FIG. 7. Pickerel-weed (*Pontederia cordata*) at Twin Lakes, Salisbury. In the background is an extensive growth of cat-tails and bulrushes.

the subjoined list are given a number of other aquatics with aerial foliage which are found in greater or less abundance growing in shallow water along mucky shores in many lakes and ponds.

Alisma Plantago-aquatica	*Pontederia cordata*
Cladium mariscoides	*Sagittaria latifolia*
Dulichium arundinaceum	*Sparganium americanum*
Orontium aquaticum	var. *androcladum*
Peltandra virginica	*Sparganium eurycarpum*

To these should perhaps be added the curious AMPHIBIOUS PLANTS, *Proserpinaca palustris*, *Sium cicutaefolium*, and *Cicuta bulbifera*,—species adapted to alternate submergence and emergence.

Most of the plants characteristic of the bulrush—pickerel-weed—cat-tail stage in the lake-swamp succession are provided with more or less extensive rhizome systems, which ramify near the surface of the mucky substratum, thereby tending to make the bottom more solid. The building up of the substratum proceeds much more rapidly as the depth of the water decreases, due partly to the denser plant population of the shoreward zones, as compared with those farther lakeward, and partly to the fact that mechanical tissues, which naturally resist decay, are much more highly developed in plants with aerial organs than in plants which are entirely or for the most part submerged.

Succession in Lake Swamps.—As soon as the bottom of a pond has been built up high enough so that the substratum is exposed during part of the year, aquatic plants begin to give way to terrestrial species. For the sake of convenience, the various stages in the succession up to this point may be referred to collectively as the LAKE SERIES, and the subsequent stages as the SWAMP SERIES. But it is manifestly impossible to draw a sharp line of demarcation between the two; for not only are various species of the bulrush—pickerel-weed—cat-tail association quite characteristic of wet swamps, but it is often easy to observe within this zone, along the shore of a lake, a gradual transition from lake on the one hand to swamp on the other. The bulrush—pickerel-weed—cat-tail stage, then, represents a connecting link between the vegetation of lakes and that of swamps. Swamps which have originated through the filling in of a lake or pond, after the manner above described, may be termed LAKE SWAMPS.

Almost always, in a succession like the one under discussion, the first true land plants to appear in the succession are sedges; hence, the first swamp stage is known as the SEDGE STAGE. To a greater degree than any of the plants that have preceded them, the sedges are equipped with tough rhizomes and copious slender roots, through the interweaving of which the soil is more firmly bound together and converted into a compact turf. By far the commonest, and ecologically the most important, sedge of Connecticut swamps is *Carex stricta*, a species which is readily recognized from its tussock-forming habit (FIG. 8); but frequently other plants with grass-like foliage are equally or even more prominent.

Among these latter, special mention should be made of the spike rush *Eleocharis tenuis*, the grass *Glyceria canadensis*, and the rush *Juncus effusus*. A swamp with predominantly grass-like vegetation is commonly referred to as a MARSH.

The sedge association is much richer in species than any of the

FIG. 8. *Carex stricta* swamp along the Farmington River, Simsbury, showing the tussock-forming habit of this sedge. Picture taken in winter.

preceding stages in the succession, but the plants are still almost exclusively herbaceous. In the subjoined list are given a number of additional vascular species commonly found here.

Acorus Calamus	*Hypericum virginicum*
Asclepias incarnata	*Impatiens biflora*
*Aspidium Thelypteris**	*Iris versicolor*
Aster novi-belgii	*Juncus acuminatus*
Bidens frondosa	*Juncus canadensis*
*Calamagrostis canadensis**	*Lycopus americanus*
*Campanula aparinoides**	*Lysimachia terrestris*
Carex filiformis	*Mimulus ringens*
*Carex lurida**	*Osmunda regalis*
*Carex stipata**	*Pogonia ophioglossoides*

Cicuta maculata
*Cyperus strigosus**
Epilobium densum
Eriophorum virginicum
*Eupatorium perfoliatum**
*Eupatorium purpureum**
Geum rivale
Ranunculus septentrionalis
Saxifraga pennsylvanica
Scirpus cyperinus
Scutellaria galericulata
*Solidago neglecta**
*Thalictrum polygamum**
*Verbena hastata**
Woodwardia virginica

A *Carex stricta* swamp might well be said to represent a composite habitat. For while the low wet areas between the tussocks afford a suitable substratum for markedly hydrophytic species like *Glyceria canadensis*, *Iris versicolor*, *Lysimachia terrestris*, and *Scirpus cyperinus*, the tussocks, higher and drier than the intervening spaces, offer a foothold for plants like *Aspidium Thelypteris*, *Calamagrostis canadensis*, *Eupatorium purpureum*, and *Verbena hastata*, which thrive best in soil that is not permanently saturated.* In sedge swamps where tussocks of *Carex stricta* are absent, the more mesophytic species, such as *Aspidium Thelypteris* and *Calamagrostis canadensis*, are for the most part restricted to the higher, drier areas, and frequently form a distinct zone around the margin of the swamp.

The sedge stage may be of short or long duration. The building up of the substratum continues, but with less speed than heretofore, due to the accelerated and more thorough oxidation of plant remains which results from exposure to the air. And just as earlier in the series submersed aquatics were shaded out, so to speak, by water-lilies, so in the competition for light the low herbaceous species of the sedge association are destined in the course of time to be superseded as the dominant type of vegetation by shrubs, and these in turn by trees. Many of the plants of the sedge stage persist into the SHRUB STAGE, but they come to occupy a more and more subordinate position. The commonest shrubs of open swamps are the alders (*Alnus rugosa* [FIG. 9] and *Alnus incana*). Indeed, an alderless swamp is a rarity. Along with the alders occur many other shrubs, the most important of which are indicated below.

* All species starred (*) in the above list belong to this latter class. Some of those not starred should perhaps also be included here, but it is very difficult to draw sharp lines.

Cephalanthus occidentalis
Clethra alnifolia
Cornus Amomum
Ilex verticillata
Lyonia ligustrina
Pyrus melanocarpa
Rhododendron viscosum
Rhus vernix
Rosa carolina
Rubus hispidus
Salix discolor
Salix sericea
Spiraea latifolia
Spiraea tomentosa
Vaccinium corymbosum
Viburnum dentatum

FIG. 9. Alders (*Alnus rugosa*) in a swamp, East Haven. View taken in January.

During the early phases of the shrub stage, certain of these shrubs may be more conspicuous than the alders. This is especially true of the *Cephalanthus*, which frequently comes in so early in the succession and occupies the territory invaded in such force that the sedge stage may be almost, if not quite, suppressed. But ultimately, because of its greater height growth, its relative tolerance of shade, and its ability to adapt itself to a wide range of soil conditions, the alder usually becomes the predominant form.

The terminal member of the lake-swamp succession is a

SWAMP FOREST, in which red maple (*Acer rubrum*) is invariably present and more often than not predominates. Commonly growing with it are *Ulmus americana*, *Betula lutea*, and *Fraxinus nigra*. In northern Connecticut the tamarack (*Larix laricina*) is an important swamp tree,* while the coast white cedar (*Chamaecyparis thyoides*) is similarly common in the eastern part of the state. Sometimes other trees, to be mentioned elsewhere (p. 193), occur in lake swamps. Several of the shrubs of open swamps are equally characteristic of wooded swamps, but the herbaceous vegetation is composed very largely of forms not heretofore noted. The following lists of species commonly represented in the undergrowth of swamp forests have been compiled from observations made in more than twenty swamps—exclusive of bogs—in various sections of the state.

WOODY PLANTS

Alnus incana	*Psedera quinquefolia*
Alnus rugosa	*Rhododendron maximum*†
Amelanchier oblongifolia	*Rhus Toxicodendron*
Benzoin aestivale	*Rubus hispidus*
Clethra alnifolia	*Rubus triflorus*
Cornus Amomum	*Sambucus canadensis*
Ilex verticillata	*Vaccinium corymbosum*
Lyonia ligustrina	*Viburnum dentatum*
Viburnum Lentago	

HERBACEOUS PLANTS

Arisaema triphyllum	*Impatiens biflora*
Aspidium cristatum	*Lobelia cardinalis*
Aspidium Thelypteris	*Lycopodium lucidulum*
Aster puniceus	*Maianthemum canadense*
Boehmeria cylindrica	*Onoclea sensibilis*
Caltha palustris	*Osmunda cinnamomea*
Carex crinita	*Osmunda regalis*
Carex stricta	*Polygonum arifolium*
Chrysosplenium americanum	*Solidago patula*

* *Thuja occidentalis*, one of the characteristic swamp trees farther north, occurs in swamps at Salisbury and Canaan.

† A prominent shrub in many of the *Chamaecyparis* swamps of southeastern Connecticut; found also in a few swamps in Tolland and Litchfield Counties.

Cinna arundinacea
Coptis trifolia
Galium Claytoni
Glyceria Torreyana
Hydrocotyle americana
Symplocarpus foetidus
Thalictrum polygamum
Veratrum viride
Viola cucullata
Viola pallens

Just as was pointed out in connection with *Carex stricta* swamps, the presence in wooded swamps of elevations, formed here by stumps, fallen trunks, roots, etc., makes possible the existence of many species which would be unable to grow in the lower, wetter situations.

The Rôle of Liverworts and Mosses in Lowland Successions.—A short digression may be made at this point to consider the part played in the succession by liverworts and mosses. These are sometimes present in great profusion and may contribute in some measure to the accumulation of humus. In the subaquatic stages of the succession they are often represented by submersed or floating species, such as *Ricciella fluitans*, *Ricciocarpus natans*, *Fontinalis antipyretica* var. *gigantea*, *Fontinalis novae-angliae*, and various forms of *Drepanocladus*. Species of *Sphagnum* may be present here as well as in the earlier swamp stages, but they are often absent and seldom develop as luxuriantly as in the bog succession which will be described presently. Common mosses of open sedge or shrub swamps are *Aulacomnium palustre*, *Bryum ventricosum*, *Philonotis fontana*, *Elodium paludosum*, *Chrysohypnum stellatum*, *Acrocladium cuspidatum*, and *Polytrichum commune*, while the liverworts *Anthoceros laevis* and *Pellia epiphylla* often grow on the perpendicular sides of *Carex stricta* hummocks. In wooded swamps the bryophytes are usually well represented, the following species being perhaps as characteristic as any.

Growing in moist or wet depressions:

Pallavicinia Lyellii
Chiloscyphus rivularis
Sphagnum sp.
Bryum bimum
Mnium punctatum
Mnium cinclidioides
Brachythecium novae-angliae
Calliergon cordifolium
Climacium americanum

Growing on stumps, logs, etc.:

Cephalozia connivens
Bazzania trilobata
Dicranum flagellare
Leucobryum glaucum

Trichocolea tomentella *Fissidens adiantoides*
Dicranum scoparium *Thuidium delicatulum*
Georgia pellucida

The Relation of Swamp Forests to Upland Forests.—In relation to the various plant societies of the lake-swamp series, the swamp forest may be regarded as at least a temporary climax, although it may not always represent the ultimate condition. So long as the ground remains saturated with water throughout a great portion of the year, it is manifestly difficult for a mesophytic flora to develop. Yet very frequently seeds of white pine (*Pinus Strobus*) and other trees from an adjoining upland germinate in a swamp during periods of protracted drought, and once firmly established these are sometimes able to persist in spite of unfavorable soil conditions. Moreover, many upland mesophytes, like *Tsuga canadensis*, *Hamamelis virginiana*, and *Kalmia latifolia*, are commonly present in such swamps, growing on elevations of various kinds. Through the extension of these elevations and the formation of new ones, it is apparent that the general level of the ground may become raised above the zone of saturation, so that mesophytes will become more numerous and the swamp plants correspondingly restricted. In this fashion it is perhaps conceivable that a swamp forest might ultimately be replaced by a forest essentially similar to that which marks the climax of succession on uplands. Theoretically, at least, such a forest represents the culmination of all hydrarch, as well as xerarch, successions in this region. But, parenthetically, it must be conceded that while upland mesophytes undoubtedly tend to become more and more abundant in a lowland forest, and while the tendency for such a forest to approach the upland type is unmistakable, nevertheless, so rapid is decomposition under subaerial conditions, that it is doubtful whether the substratum is ever raised sufficiently to produce a truly mesophytic habitat through the operation of biotic factors alone.

Variations in the Rapidity of Succession in Lakes.—In the foregoing paragraphs it has been shown that there is a tendency for lakes and ponds to become filled in and converted into swamps through the activity of vegetation; but there are great differences in the rate at which this transformation is brought about. Thus

while many ponds have become completely clogged up through the accumulation of muck or peat, there are others in which scarcely any such accumulation would appear to have taken place. And between these two extremes are ponds which exhibit various intermediate degrees of filling. Although the reason for this discrepancy between different ponds is not clear at the present time, it may be due merely to the chance failure of certain plants to become established in the "barren" lakes as soon as in the "fertile" ones. Or it is quite conceivable that a paucity of organic debris may be due to the existence of environmental conditions unfavorable to the luxuriant development of aquatic plants. Certain it is that in ponds with a sandy, gravelly, or rocky bottom, i. e., in ponds where muck or peat has failed to accumulate, the vegetation invariably is sparser than in ponds with a mucky bottom. Particularly is there a dearth here of those species most active in peat formation, such as the larger pondweeds, the water-lilies, the pickerel-weed, and the cat-tail. The vegetation along the sandy or gravelly shores of such a pond is quite different from that along mucky shores. Representative species are *Eriocaulon septangulare*, *Najas flexilis*, and *Lobelia Dortmanna*—growing in shallow water; and *Panicum agrostoides*, *Cyperus dentatus*, *Cyperus strigosus*, *Eleocharis acicularis*, *Juncus brevicaudatus*, *Hypericum mutilum*, *Lysimachia terrestris*, *Gratiola aurea*, and *Gnaphalium uliginosum*—growing on the shore. The factors directly or indirectly responsible for the assumed adverse environmental conditions referred to above may possibly be many. Among those that may enter in are the depth of the water body, the temperature and clearness of the water, the steepness of the shores, the amount of inorganic detritus washed in by streams or otherwise, and the source of water supply. That the degree of protection from or exposure to wind, and the nature of the water currents may also be important factors is suggested by the fact that mucky and sandy shores often occur around the margin of the same lake, the former in the more sheltered, the latter in the more exposed situations. Failure of peat to accumulate might also of course result from any conditions which would promote rapid and complete decomposition; or locally it might be effected through the removal of plant remains by water currents.

Succession in Spring Swamps.—Many swamps have arisen through the filling in of lakes and ponds in the manner described. But a large proportion of Connecticut swamps, as already pointed out (pp. 173–175), owe their origin to the relation between topography and ground water level. The former type of swamp has been referred to as a lake swamp. In contrast to this, the latter type of swamp, by reason of the fact that its existence depends on the presence of seepage or spring water, may be called a seepage or SPRING SWAMP. In a spring swamp there of course are never any truly aquatic stages in the succession. Terrestrial plants are present from the very outset. In a PERMANENT SPRING SWAMP the pioneer association is commonly dominated by sedges, rushes, and grasses, and in general its composition conforms closely to that described for the sedge stage of the lake-swamp succession. But in a PERIODIC SPRING SWAMP the pioneer association may be quite different, both floristically and in its general aspect, from that of a permanent swamp. To be sure, many of the plants characteristic of permanent swamps are represented here also, but on the whole the vegetation is much more mesophytic. Perhaps as good an illustration of a periodic swamp as can be selected is afforded by a LOW MEADOW. Such an area may be very wet in winter and spring, but later in the season the surface layers of the soil usually become relatively dry. As in permanent swamps, the predominant vegetation here is grass-like, but many other herbaceous plants are also conspicuous. The list of species given below may be considered as fairly representative of meadows.

Agrostis alba
Anthoxanthum odoratum
Calamagrostis canadensis
Carex lurida
Carex scoparia
Carex stellulata
Carex stipata
Carex stricta
Castilleja coccinea
Cyperus strigosus
Eupatorium perfoliatum
Eupatorium purpureum
Gentiana crinita
Glyceria nervata
Juncus effusus
Poa pratensis
Rhexia virginica
Rynchospora glomerata
Sanguisorba canadensis
Selaginella apus
Thalictrum polygamum
Verbena hastata
Vernonia noveboracensis
Veronica virginica

Two types of meadows might be distinguished, viz., wet meadows and dry meadows. But the two are not sharply delimited from one another, and it is hardly worth while here to attempt to treat them separately. Owing to their suitability for the growth of grasses, meadows, especially the drier ones, are commonly cultivated and cut over annually for hay, and much of their natural vegetation is thereby eliminated.

The shrub stage in a permanent spring swamp closely approximates the corresponding stage in a lake swamp. The tree stage likewise is quite similar, although some of the trees to be mentioned presently as characteristic of periodic swamps frequently occur here also. In periodic spring swamps the shrub stage in the succession scarcely differs from the shrub stage in permanent spring swamps, except for the scarcity or absence of markedly hydrophytic species like *Cephalanthus*, the greater abundance of the spiraeas and some others of the less hydrophytic shrubs, and the frequent occurrence of mesophytic shrubs. In northwestern Connecticut *Potentilla fruticosa* is very characteristic of such areas. But the tree stage in periodic swamps exhibits noteworthy differences as compared with the tree stage in permanent swamps. For, while any of the trees listed as characteristic of permanent swamps may be found here also, and while here as there red maple and elm may be the predominant species, the forests of periodic swamps are characterized by the presence of a number of trees which require an abundant water supply, but which do not thrive well in a permanently saturated soil. Among these may be mentioned *Tsuga canadensis*, *Carya cordiformis*, *Carpinus caroliniana*, *Quercus bicolor*, *Quercus palustris*, *Liriodendron Tulipifera*, *Nyssa sylvatica*, *Fraxinus pennsylvanica* and *Platanus occidentalis*. The herbaceous vegetation of such swamps includes species which are seldom found in permanent swamps, such as *Erythronium americanum*, *Dentaria diphylla*, and *Panax trifolium*.

As concerns the building up of the substratum to a higher level through the accumulation of plant remains, a state of equilibrium somewhat analogous to that observed in many lakes is very commonly encountered in clayey or sandy swamps where, for various reasons, dead organic matter oxidizes so rapidly that humus fails to collect. Particularly is this true of periodic swamps. In a colder,

more humid climate, peat might develop on such sites; but in Connecticut the mineral soil is frequently covered by little more than the thin mantle of living vegetation and there is little humus. Humus, as is well known, possesses a very high capacity for retaining water, so that a soil rich in humus dries out very slowly. A soil poor in humus may be equally wet in spring, but with the lowering of the water table it dries out much more quickly. Such a swamp, in consequence of the better drainage and aeration of the soil, must necessarily afford a habitat quite different from that in a swamp underlain by a mucky soil. It seems probable, therefore, that the abundance or scarcity of humus may be an important factor in restricting the distribution of the trees mentioned above as characteristic of periodic swamps.

Intermittent Ponds.—From an ecological standpoint these should be classed as swamps rather than ponds, since the seasons when their basins contain water coincide for the most part with the period of vegetative inactivity. During the growing season, except for a short time in spring and early summer, the bottom is merely muddy, and very often in late summer it is quite dry. With the exception of species having more or less amphibious proclivities, like *Proserpinaca palustris*, *Ludvigia palustris*, *Alisma Plantago-aquatica*, *Sium cicutaefolium*, and occasionally *Nymphaea advena*, aquatic plants are absent. Those parts of the bottom which remain longest submerged may be almost destitute of vascular plants and frequently support a rich growth of algae, like *Vaucheria* and *Botrydium*, or of bryophytes, like *Riccia*, *Fossombronia*, and *Ephemerum*. On parts of the bottom which are exposed during a somewhat longer period commonly grow *Eleocharis acicularis*, *Hypericum virginicum*, *Lysimachia terrestris*, etc.; while very often there is a rank growth of various species of *Bidens* and *Polygonum*, together with other rapid-growing, fall-flowering annuals. Fringing the margin of the "pond" may occur almost any of the herbs, shrubs, or trees characteristic of swamps. It should be noted, perhaps, that *Cephalanthus* is an almost omnipresent marginal shrub.

PLANTS IN RELATION TO THE FORMATION OF MARL

There is one other important phase of plant activity in connection with the filling in of lakes and ponds to which no ref-

erence has yet been made, namely, the formation of marl. Marl deposits are always associated with calcareous regions, and in Connecticut are confined to the limestone areas in the western part of the state. At Twin Lakes, Salisbury, there are quite extensive deposits, estimated in places to exceed a hundred feet in depth, and there are similar deposits near Danbury and elsewhere. Chemically, pure marl contains about ninety-five per cent. of calcium carbonate. Formerly such deposits were supposed either to represent shell remains, or else to have originated through mechanical sedimentation or chemical precipitation from calcium-containing waters.* But while the presence in marl beds of *Chara* and other plant "fossils" had frequently caused comment, and although it is a common observation that in lakes where marl is being deposited, submersed aquatic plants are usually coated with a thin crust of calcium carbonate, it remained for Davis† to demonstrate the important rôle played by plants, particularly by the alga *Chara*, in marl formation.

In a general way it may be asserted that plants are able to bring about the formation of marl by causing the precipitation of various calcium salts which may occur dissolved in the waters of lakes and ponds. Two methods by which plants may effect this result are easily conceived. (1) The abstraction of carbon dioxide from water in which calcium is present in excess, held in solution by free carbon dioxide, would cause the precipitation of the calcium salts. (2) The combination of the oxygen liberated by plants with easily soluble salts like calcium bicarbonate, thereby converting them into less soluble salts like calcium carbonate, would result in precipitation. The existence of still a third, and possibly even more effective, method of calcium concentration has been pretty conclusively demonstrated by Davis in the case of *Chara*. (3) The calcium accumulates in the cells of this plant in the form of calcium succinate, one of the few water-soluble salts of calcium. Later on, although just how is not as yet wholly understood, the dissolved salts are excreted and deposited in

* For further discussion, see Hale, D. J., Theories of origin of bog lime or marl. Geol. Surv. Michigan 8^3: 41–64. 1903.

† A contribution to the natural history of marl. Geol. Surv. Michigan 8^3: 65–96. 1903. Also earlier papers in Journal of Geology.

an insoluble form on the surfaces of the cells. At Twin Lakes this alga is extremely abundant, more so than in any other lake or pond in the state, so far as the writer's observations have extended. Here, not only *Chara*, but the leaves and stems of *Najas*, *Elodea*, and various species of *Potamogeton* are incrusted by a thin, white, flaky deposit of marl. Some of the blue green algae, notably *Zonotrichia*, are likewise instrumental in causing marl formation.* Because of the inability of most of the plants active in its precipitation to survive in competition with shallow water species, the production of marl is largely restricted to the deeper parts of lakes.

THE FLOATING MAT

Occurrence and Importance of the Floating Mat.—In an earlier paragraph the writer has alluded to the manner in which the shallow-water zones of vegetation in a lake tend to push out from the shore and to encroach upon the deeper areas. In most lakes and

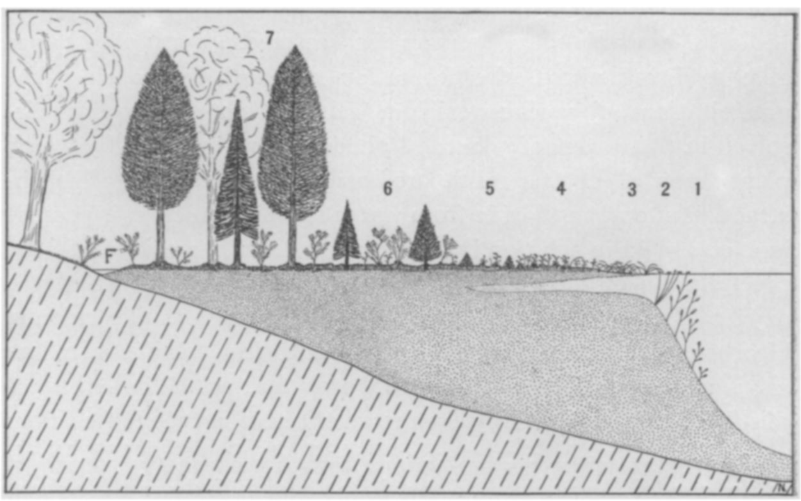

FIG. 10. Diagrammatic vertical section through the marginal portion of a lake which is being filled in through the intervention of a floating mat, showing the usual succession of plant societies. Sequence of Zones: 1. Pondweed Zone; 2. Water-lily Zone; 3. *Decodon* Zone; 4. Cassandra—*Sphagnum* Zone; 5. Cassandra—*Sphagnum*—Sedge—Low Spruce Zone; 6. Tall Shrub Zone; 7. Bog Forest. F = Marginal Ditch or "Fosse".

* For detailed discussion of the relation of *Chara* and *Zonotrichia* to marl formation, see Davis, 1903, *op. cit.*, especially pp. 87–92.

ponds where rapid peat accumulation is taking place the filling in of the deeper waters is brought about in this manner. Very often the growth of certain marginal swamp plants is so vigorous as to give rise to a raft-like zone of vegetation which spreads out from the shore over the surface of the water, and which is commonly referred to as a FLOATING MAT (FIG. 10). There will be described next, then, the manner in which this mat is developed, together with the succession of plant associations which accompanies the process. And since in Connecticut the floating mat succession is commonly associated with bogs, a type of swamp not yet treated, the two will be considered together, i. e., the succession is assumed to culminate in the formation of a bog.

Mat Formation due to Sedges.—The lake stages in such a succession are identical with those already described. There may thus appear, in order, submersed aquatics, aquatics with floating leaves, and aquatics with aerial foliage; but, due to the encroachment of the mat, these stages may be quite abbreviated, and one or all may be eliminated. It is in the transition from lake to swamp that the floating mat comes into play. According to the conception which has been widely circulated, especially in geological literature previous to 1907, this mat is formed in the following manner. "Certain mosses, particularly those of the genus *Sphagnum*, have a habit of growing out on the water surface and forming a mat of intertwined stems connected with the shore. At this stage the lake is an open water body with a border of vegetation floating near the rim. Gradually this rim of moss creeps toward the center of the pond until it is completely closed in and covered over with a layer of vegetation. The lake is now a swamp; and such a swamp, with a floating layer of aquatic plants, is known as a 'quaking bog'; it is possible in some cases to walk across an old lake on a mat of vegetation while the water remains below. These mosses have a habit of growing at the top while the old stems are dying below, and the rotted fragments drop to the bottom of the pond and help to fill it up."*

Except for the stress laid on the rôle of *Sphagnum* and other mosses, the description above quoted portrays the origin and behavior of the floating mat fairly accurately; and for cold,

* Rice, W. N., and Gregory, H. E., *op. cit.*, p. 249.

humid regions like parts of eastern Canada the importance of the mosses would hardly be overestimated. But, as indicated by Transeau* and conclusively proved by Davis,† in milder, less humid regions the mosses play at best a very subsidiary part in mat formation. In Michigan, according to these authorities, the most important mat-forming plants are the sedges, particularly *Carex filiformis*. This species is capable of spreading rapidly by means of rhizomes. As pointed out by Davis, these subterranean or subaquatic stems will often grow horizontally a foot or more in length during a single season, producing at the nodes an abundance of tough, slender roots, and bearing at their tips terminal buds "from which new plants rise to send out in turn a new series of horizontal stems. When conditions are un-

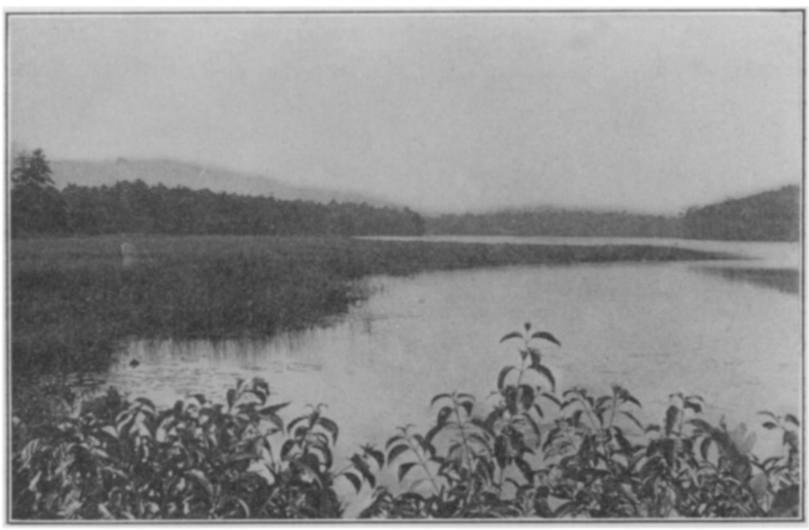

FIG. 11. Floating sedge mat at Twin Lakes. The plants along the margin of the mat are bulrushes.

favorable for the rhizomes to grow outward into open water, they sometimes grow diagonally downward over the edge of the mat, and thus the mat is strengthened as well as extended by the growth of the plant." On account of its low specific gravity, the tangle of roots and rhizomes thus produced floats on the surface of the

* Bot. Gaz. 40: 363. 1906.

† 1907, *loc. cit.*, pp. 135–138.

water like a raft. Along the western shore of one of the Twin Lakes is a beautiful example of a floating mat which thus owes its origin to *Carex filiformis* (FIG. 11); and similar mats are frequently encountered in other sections of the state. Toward its lakeward margin such a mat is usually thin, but farther away from the edge it reaches a thickness of two feet or more and becomes firm enough to support considerable weight. For some distance from its outer margin, in cases where it is typically developed, the mat is actually floating and is underlain by clear water. But in proceeding from the margin shoreward the water underneath is "found to become more and more full of finely divided matter until, at a variable distance from the water's edge, the deposit is nearly solid and the mat no longer floats".* The filling up of the open water underneath, and the ultimate grounding of the mat is brought about very largely in the manner already suggested, namely, by the dropping down of debris from the lower surface of the raft. Often, owing to local conditions, the mat grows outward from the shore so slowly that the water beneath the floating substratum becomes filled out to its very margin. By the time the mat has grounded, if not before, shrubs have asserted themselves as the controlling element of surface vegetation; and these in turn, as in the lake-swamp succession already described, ultimately give way to trees.

Mat Formation due to Decodon.—But, on the whole, in Connecticut the sedges are overshadowed as pioneer mat formers by certain shrubs, notably *Decodon verticillatus*. The manner in which this latter shrub not only brings about the formation of a floating mat but accelerates the upbuilding of the surface as well, has been admirably described by Davis.† Growing at the water's edge it sends up slender, arching stems, many of which reach out over the open lake, curving gracefully downward toward their tips until they enter the water (FIG. 12). Here the stem becomes greatly swollen, due to the formation of aerenchyma, and develops numerous adventitious roots. The aerial part of the plant is herbaceous and dies at the end of the growing season. But the swollen, submerged portion of the stem becomes woody and perennial, lives through the winter, moored in place, as it were, by the other-

* Davis, 1907, *loc. cit.*, p. 138.

† 1907, *loc. cit.*, pp. 151, 152, 204–206.

wise functionless, dead aerial part of the stem, and the following season sends up a fresh series of aerial stems. Some of these grow outward over the open water, thus extending the margin of the mat lakeward; others reach shoreward, thereby more effectually uniting the newer with the older portions of the mat; while yet others grow out in lateral directions, in this way binding together

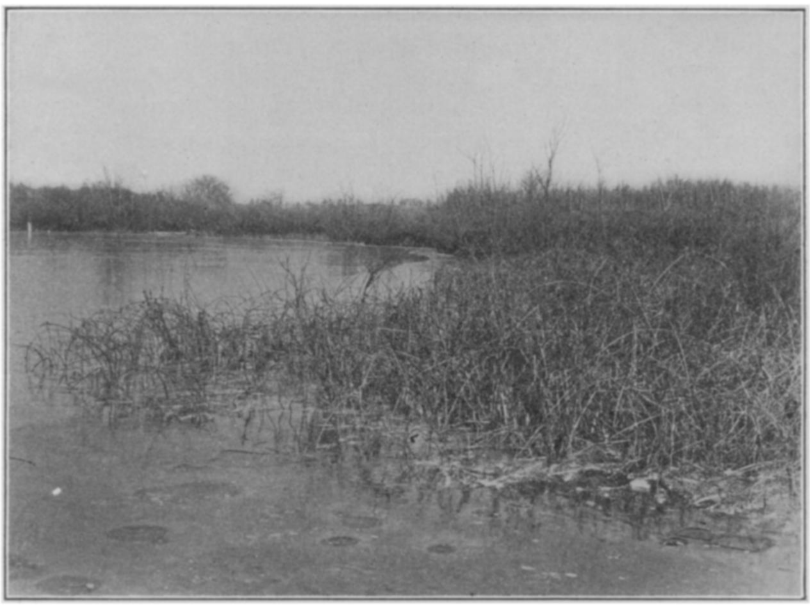

FIG. 12. *Decodon verticillatus* advancing into open water along margin of a pond, Southington. View taken in winter.

more firmly the integral parts of the still rudimentary structure. At this stage the mat is little more than a framework, consisting of a loose aggregation of the *Decodon* plants. But upon the stools formed by the *Decodon*, and about its roots, other plants soon appear, and as these increase in number, reaching across from one stool to another, the skeleton gradually becomes transformed into a continuous, compact body.

Importance of Other Plants in Mat Formation.—Often one of the earliest plants to appear among the *Decodon* stools is the *Sphagnum*. But while this moss may act as a space filler, it adds little to the strength of the mat; for its stems, weak and nearly

devoid of mechanical tissue, could hardly be expected to possess any great degree of tensile strength. Moreover, as a rule, *Sphagnum* does not develop in any abundance until a later stage in the succession. Various species of *Drepanocladus* may also grow in the water about the *Decodon* roots, but their rôle in mat formation is inconsequential. As in the case of the sedge mat earlier described, it is the vascular plants with their tough stems and roots, particularly species like the cranberry (*Vaccinium macrocarpon*) and cassandra (*Chamaedaphne calyculata*), which are primarily responsible for the increase in the continuity and compactness of the substratum. *Decodon* is primarily a pioneer, and in competition with other plants is speedily exterminated. When present, it usually occupies a zone from six to a dozen feet wide along the water front, but, except for scattered specimens, is absent elsewhere. Inside the *Decodon* zone there is commonly a zone dominated by cassandra, along with which, in increasing abundance, grows the *Sphagnum*.

It might naturally be anticipated that where the pioneer plants are shrubs, the sedges would be eliminated from the succession, but this is rarely the case. Almost always sedges and other herbaceous bog plants occur in among the shrubs, and quite frequently the cassandra zone is bordered on the landward side by a more or less continuous zone in which the dominant plants are *Sphagnum*, cranberries, and such sedges as *Rynchospora alba* and *Eriophorum virginicum*. The exact explanation of this last mentioned phase in the succession is puzzling. It seems to represent a RETROGRESSIVE CONDITION due to some disturbance which has caused the disappearance of the cassandra and has thus created an opening for a more primitive association to become established. Such a result might be effected either by a sinking of the mat, or by a temporary elevation of the water level which might flood the grounded portions of the mat, and, if of sufficient duration, might cause the death of the cassandra. Proceeding farther landward from this zone, shrubs once more assume control, and under normal conditions, as in other cases, trees ultimately become the predominating element of the vegetation.

There are other ways in which the formation of a floating mat may be inaugurated. At Bingham Pond, Salisbury (FIG. 14), and

elsewhere (FIG. 15) the plant which fringes the water's edge and forms the skeleton for the advancing mat is the cassandra. The extension outward into the open water is slow when dependent on this plant, and the mat is usually thick and firm out to its very edge. At Bailey Pond, Voluntown, is a remarkable submersed mat, some ten feet wide, composed entirely of the rhizomes of the fern *Woodwardia virginica*. Floating logs, sticks and similar debris doubtless contribute their quota to the formation of the raft; while sometimes great patches of rhizome-permeated muck break loose from the bottom of a pond, rise to its surface, and furnish a substratum favorable for the rapid spread of sedges and other mat forming plants.*

ECOLOGICAL RELATIONS, ORIGIN, AND DISTRIBUTION OF BOGS

Bogs Compared with Ordinary Swamps.—A BOG may be defined as a fresh water swamp characterized, especially in the shrub stage, by an abundance of xerophytic plants. It might well be designated a XEROPHYTIC SWAMP. In Connecticut, so far as known, bogs are always developed in morainal depressions. This type of swamp, by reason of its unique vegetation, the ecological problems involved, and the economic value of the frequently underlying peat deposits, has probably received more attention at the hands of investigators than all other swamp types put together. In comparing the plant associations encountered in a lake-bog succession with those in an ordinary lake-swamp series, the first appreciable differences are perceived in the sedge stage, while the departure of the two types from one another becomes very pronounced in the shrub and tree stages. From a floristic standpoint, Connecticut bog vegetation is unique because of the predominance of ericaceous shrubs, the prevalence of black spruce (*Picea mariana*) and other boreal species otherwise absent from this region, the presence of bizarre forms like the pitcher plant (*Sarracenia purpurea*) and the sundews (*Drosera rotundifolia* and *Drosera longifolia*), and the usually luxuriant development of *Sphagna*. Ecologically, the most interesting problems relate to the phenomenon of bog xerophytism.

* Such masses often rise to the surface during the summer, only to sink to the bottom again in the fall. In this connection see S. Powers's paper on "Floating Islands", Bull. Geog. Soc. Philadelphia 12: 1–26. *f. 1–9.* 1914.

Succession of Plant Societies in Bogs.—As suggested in earlier paragraphs, succession in bogs, in Connecticut at any rate, is usually associated with floating mat formation, and several of the phenomena of a bog succession have already been discussed under that head. Where a bog still borders an open body of water the various plant associations mentioned in connection with the floating mat succession are often clearly distinguishable. But quite as often, especially where the bog occupies a basin that has become completely filled in (FIG. 13), the three associations are

FIG. 13. Spruce bog, Willington. *Picea mariana* and *Chamaedaphne calyculata* the dominant forms; small, scattered specimens of *Pinus rigida* in the foreground.

more or less completely merged into one, i. e., they are telescoped. The shrubs here, along with *Sphagnum*, tend to form elevated patches; sedges, with *Sphagnum*, dominate on the intervening lower ground; while the spruces—seldom over fifteen feet high, mostly under eight, and commonly less than four—for the most part grow scattered about among the shrubs, here and there developing colonies of sufficient size and density to shade out the more in-

tolerant undergrowth. In a bog of this sort the more depressed, wetter spots may be occupied largely by various bryophytes, e. g., *Cephalozia fluitans*, *Mylia anomala*, *Scapania irrigua*, *Aulacomnium palustre*, *Acrocladium cuspidatum*, *Drepanocladus fluitans*, and certain species of *Sphagnum*. The following herbaceous seed plants also commonly occur in like situations.

Arethusa bulbosa	*Hypericum virginicum*
Calla palustris	*Menyanthes trifoliata*
Drosera longifolia	*Rynchospora alba*
Drosera rotundifolia	*Scheuchzeria palustris*
Dulichium arundinaceum	*Smilacina trifolia*
Eleocharis palustris	*Utricularia cornuta*

Xyris caroliniana

The vegetation of these depressions may represent a relict of a primitive stage in the succession, but it seems more likely that it represents a retrogressive phase like the one already described. Characteristic also of open bogs, but mostly growing in less wet places, are the following herbaceous species.

Asclepias incarnata	*Epilobium* sp.
Aspidium Thelypteris	*Eriophorum* sp.
Calamagrostis canadensis	*Habenaria blephariglottis*
Carex rostrata	*Lysimachia terrestris*
Carex trisperma	*Pogonia ophioglossoides*
var. *Billingsii*	*Woodwardia virginica*

From these lists are omitted purposely a number of species, like *Carex pauciflora* and *Carex paupercula*, which are peculiar to bogs but which have been recorded from only one or two localities in the state.

The shrubs of open bogs may conveniently be divided into two groups, somewhat as follows.

FIRST GROUP

Andromeda glaucophylla	*Gaylussacia baccata*
Chamaedaphne calyculata	*Kalmia angustifolia*
Chiogenes hispidula	*Kalmia polifolia*
Gaultheria procumbens	*Ledum groenlandicum*
Gaylussacia dumosa	*Vaccinium macrocarpon*
var. *Bigeloviana**	*Vaccinium Oxycoccus*

* This northern variety of *Gaylussacia dumosa* was described by Fernald in Rhodora 13: 95–99. 1911.

SECOND GROUP

Alnus rugosa (or *A. incana*)	*Pyrus melanocarpa*
Amelanchier oblongifolia	*Rhododendron viscosum*
Ilex verticillata	*Rhus vernix*
Myrica carolinensis	*Vaccinium corymbosum*
Nemopanthus mucronata	*Viburnum cassinoides*

Most of the shrubs peculiar to bogs are included in the first group. It will be noted that all of the species there listed are ericaceous, and that practically all of them are distinctly northern in their range. The shrubs in the second group are not so strictly confined to bogs, but, with one or two exceptions, are frequent or common in swamps of the ordinary type. The majority of them are equally well developed far to the south. It should be added that the species in the first group are comparatively low growing—mostly less than three feet high when mature—while those in the second group average well above three feet. In studying their distribution in an open bog, it is noticeable that the lower shrubs comprising the first group are pretty uniformly distributed throughout, while the taller shrubs which comprise the second group are best developed toward the landward margin, or in slightly elevated situations. In the case of a bog bordering an open pond, as at Bingham Pond (FIG. 14), there are usually four rather definite bands of woody vegetation, paralleling the water's edge: first, a zone of low shrubs; then, a zone of low shrubs intermixed with young spruces and tamaracks;* next, a zone of taller shrubs along with older trees; and finally, farthest removed from the pond, a zone of large spruces together with some of the more tolerant of the taller shrubs. Undoubtedly some correlation exists between the position usually occupied by shrubs of the second group in bogs and the fact that most of them quite commonly occur in swamps of the ordinary type, a correlation which almost certainly relates to soil aeration and drainage. There very likely is also some connection between this local distribution of these plants in bogs and swamps and their geographic distribution.

Sphagnum and its Relations.—Occasionally, as for example at Twin Lakes, a bog is encountered from which apparently *Sphagnum* is entirely missing. In the particular case cited the bog is under-

* Between this and the next shrub zone is frequently interpolated the *Sphagnum*—cranberry—sedge zone already mentioned.

lain by marl, and since *Sphagnum* is reputedly calciphobous, it was at first thought that here, at least, its absence could be easily accounted for. But in a nearby swamp which likewise overlies a calcareous subsoil *Sphagnum* is abundant. Similar observations by Davis* in Michigan, together with the experimental evidence advanced by Transeau and Weber† would make it appear highly improbable that the presence or absence of *Sphagnum* can be correlated with the presence or absence of lime. As a rule, in the floating mat succession, *Sphagnum* seldom precedes the shrubs and sedges, except to an inconsequential degree. There are a few ponds in southeastern Connecticut where *Sphagnum macrophyllum*, a remarkable southern coastal-plain species with leaves fully half an inch long, constitutes an important part of the free-floating vegetation. But this condition is exceptional. In a bog the *Sphagnum* usually appears first as a superficial layer growing on the surface of the shrub or sedge mat; but once established it often develops so rapidly and luxuriantly as to exert a profound influence on the character of the bog vegetation.‡ Growing upward in dense masses around and among the stems of various shrubs, etc., this plant commonly forms cushions which sometimes rise as much as two feet above the original water level. Antecedent plants which are unable to accommodate themselves to this change in environmental conditions are gradually eliminated.

Broadly speaking, the ability of a plant to exist in a bed of rapidly growing *Sphagnum* may be said to depend on its ability to keep pace with the upward growth of the moss. The necessity of keeping the foliage above the surface of the substratum is too obvious to require more than passing mention. But it seems very likely that it is equally important that the roots of the plant be kept above the zone of permanent saturation. For as the *Sphagnum* plants grow upward, dying away below, the lower part of the cushions becomes more and more compact and, due largely to the well-known capacity of *Sphagnum* stems and leaves for sucking in water, acting like a sponge, it becomes completely saturated. As the *Sphagnum* cushions increase in height, then,

* 1907, *loc. cit.*, p. 276.

† See Transeau, 1906, *loc. cit.*, p. 32.

‡ In this connection see also W. S. Cooper's discussion of the behavior of *Sphagnum* in Isle Royale bogs. Bot. Gaz. **55**: 200–206. 1912.

the water level rises correspondingly, with the result that the roots of plants originally growing on the mat's surface are submerged. The characteristic plants of SPHAGNUM BOGS are those which are able in some way to develop root systems above this zone of saturation. Species like *Aspidium Thelypteris* and many sedges accomplish this result through the upward growth of their rhizomes. Sprawling vines like *Chiogenes* and *Vaccinium macrocarpon* similarly have little difficulty in establishing fresh footholds from time to time. The pitcher plant possesses little power of stem elongation and individual plants are buried quite rapidly, but like some other bog plants it reproduces itself with sufficient rapidity by means of seeds to enable it to hold its own. Among the shrubs the most successful species are those which freely produce adventitious roots from the old upright stems above the zone of permanent saturation. Among others, *Chamaedaphne*, *Kalmia polifolia*, and *Ledum* are noteworthy in this respect. In a specimen of *Ledum*, for example, which the writer collected in a *Sphagnum* bog at Norfolk, the leafy shoot rose but eight inches above the surface, the remaining part of the stem, more than three feet long, being imbedded in the moss. Adventitious roots had developed throughout the length of the stem, those on the first foot of stem below the surface being vigorous and obviously the only ones functional at the time of collection. It is interesting to note in this connection that Cowles,* in his study of the vegetation on the sand dunes of Lake Michigan, found that the ability of many woody plants to withstand burial by sand likewise depends on their power of stem elongation plus the development of adventitious roots. The upward growth of a *Sphagnum* cushion proceeds most rapidly at first; eventually it attains a height where the balance between increasing evaporation and decreasing water supply is such that further upward growth is no longer possible. When this stage is reached species of the lichen *Cladonia* and relatively xerophytic mosses like *Polytrichum commune* and *Hypnum Schreberi* frequently establish themselves on top of the *Sphagnum* cushions.

The Significance of the Marginal Ditch.—Separating the bog from the adjoining upland, more often than not, there is a broad,

* Bot. Gaz. 27: 384. 1899.

open ditch, or fosse, which at certain seasons of the year may be filled with water to a depth of one or two feet. This ditch is a widespread feature of bogs and its significance is not yet wholly clear. But of the various explanations offered, that suggested by Davis* seems to the writer most plausible. Davis attributes the formation of the fosse to "the fluctuation of the water level through rather brief intervals and the constant recurrence of these fluctuations. These are attendant upon the variations in the rainfall, and the water level in the lakes and depressions may vary one, two, or more feet every few years, and may remain at the low water stage for several years in succession. . . . It is also a matter of observation that, during dry times, the water does disappear from these marginal ditches for long periods during the summer and autumn, the bottoms becoming quite dry, and this has the effect of destroying much of the hydrophytic vegetation which has established itself and also of thoroughly decomposing and disintegrating the organic matter which has accumulated during periods of high water." In this way the surface is lowered "below that of the area directly above the zone of permanent water, which, being covered by a thicker layer of vegetable debris, is kept wet by the upward capillary movement of the water from below its surface."

The Tree Stage in Bogs.—The most distinctive feature of the tree stage in Connecticut bogs, considered collectively, is the presence of the black spruce. Commonly associated with this, and sometimes forming considerable forests in the older, better drained portions of the bog, grows the tamarack. The tamarack is not so tolerant of shade as the black spruce, but its more rapid and greater height growth enable it to maintain its own in the competition for light. More or less extensive tamarack forests formerly occurred in bogs at New Fairfield, Suffield, and elsewhere. Due to the rather open character of such forests, and the slight shade produced by the tamarack, the spruce, together with much of the undergrowth present in the adjoining parts of the open bog persists here. The black spruce itself seldom forms a stand of sufficient height and density to merit the title of forest; but in the cool highlands of northwestern Connecticut, about Bingham Pond

* 1907, *loc. cit.*, p. 151. For references to other explanations see Cooper, *loc. cit.*, p. 203.

(FIG. 14), there is a magnificent forest of spruce. Here, however, the black spruce of the opener parts of the bog seems to have been largely superseded by the red spruce (*Picea rubra*), a species which attains a much larger size, but which is absent from most sections of the state.* Along with the spruce in this Bingham Pond forest

FIG. 14. Spruce bog surrounding Bingham Pond, Salisbury. Behind the marginal fringe of *Chamaedaphne*, etc., is seen the bog forest, largely composed of *Picea rubra*. Water of pond somewhat lowered through artificial drainage.

grow the mountain ash (*Pyrus americana*), a species sometimes found in bogs in other sections of the state, and commonly in bogs farther north. There are also scattered yellow birches, but the spruce predominates, casting a shade so dense as to effectually exclude nearly all of the herbs and shrubs characteristic of the open bog. The ground beneath in many places is carpeted with various mosses and liverworts, e. g., *Bazzania trilobata*, *Dicranum scoparium*, *Dicranum undulatum*, *Leucobryum glaucum*, *Hylocomium splendens*, *Ptilium Crista-castrensis*, *Stereodon imponens*,

* The correctness of the identification of these trees as *Picea rubra* is possibly open to question. At the time this forest was studied, the writer assumed them to be *Picea mariana*. Since then, however, study of these two species in the Canadian woods has led to the conviction that they must be *Picea rubra*, an opinion which was first expressed and has recently been reaffirmed by Dr. C. A. Davis. These trees also grow on the mountain slopes in the vicinity of the pond.

Hypnum Schreberi, and *Georgia pellucida*, and there are occasional patches of *Sphagnum*. Characteristic herbaceous plants here are *Aralia nudicaulis*, *Clintonia borealis*, *Coptis trifolia*, *Cypripedium acaule*, and *Maianthemum canadense;* these grow for the most part in the least shaded spots. The commonest shrub is *Kalmia latifolia*.

In eastern Connecticut, the coast white cedar largely supplants the black spruce as the characteristic bog conifer, while throughout the state bogs are frequently encountered from which conifers are entirely absent. At Berlin, for example, there is a large bog, perhaps sixteen acres in extent, whose surface, except for a peripheral band of red maple and taller shrubs, is entirely covered with heaths and *Sphagnum*. In Beaver Swamp, a bog within the New Haven city limits, red maple is likewise the only arborescent species present. The omnipresence of this latter tree in swamps of the ordinary type has already been commented on. This observation may be extended to include bogs; but here, except where the original vegetation has been disturbed, it is usually conspicuous only toward the landward margin.

The Problem of Bog Xerophytism.—In attempting to explain the differences between bog vegetation and that of ordinary swamps, two sets of factors must be taken into account, namely, factors which are active at the present time, and factors which have operated during the past. The immediate effect of the first set is seen in the phenomenon of bog xerophytism; the effect of the second set may be reflected in the restriction to bogs of so many boreal plants. That, despite their physical wetness, the soil conditions in bogs are conducive to xerophytism has long been recognized. This xerophytism is evidenced by the fact that many of the commonest bog plants are likewise characteristic of habitats which are physically dry. Thus, in Connecticut, *Gaylussacia baccata* and *Gaultheria procumbens* grow abundantly in dry woods and clearings; *Kalmia angustifolia* and *Myrica carolinensis* flourish on dry, open hillsides; while *Pyrus melanocarpa* and *Vaccinium corymbosum* are among the commonest shrubs on exposed, rocky ledges along the coast. Moreover, many of the more distinctive bog plants, in contrast with most plants of ordinary swamps, exhibit structural peculiarities which are char-

acteristic of xerophytes; while analogous xerophytic modifications may frequently be observed in the leaves of bog-grown individuals of such a species as *Alnus rugosa*, which occurs in both types of swamps. The xerophytic peculiarities of the leaves of bog evergreens, e. g., the cassandra, however, need not necessarily be attributed to the nature of the habitat, but may rather, to a certain extent at any rate, be associated with protection from excessive transpiration during the winter.*

Many theories have been advanced with a view to explaining the condition of physiological xerophytism prevalent in bogs. It has been variously ascribed to the acidity of the soil, to the low temperature of the soil, to the insufficient aeration of the soil, and to the accumulation in the soil of root excretions or various toxic substances.† Doubtless there are still other factors whose effect may be equally potent. For example, in view of the low diffusion properties of humus soils, which to a great extent would exclude salts derived from the subjacent mineral soil, together with the only partial decomposition of vegetable remains in bogs, it is conceivable that an actual scarcity in the bog substratum of the requisite mineral elements in form suitable for absorption and assimilation by most plants may be a factor of some significance. Indirectly, the topographic relations of bogs are considered important. Bogs usually develop in undrained or poorly drained depressions, and almost invariably in connection with a water body of considerable depth. In Salisbury, Norfolk, Kent, Litchfield, and elsewhere there are bog-bordered lakes, but in many cases, the depressions occupied by bogs, although quite deep, are only a few acres in extent. In two small bogs at Southington, for example, the writer was unable to touch bottom with a twenty-five foot peat sampler. One of these bogs is shown in FIG. 15. That the lack of drainage in such basins would tend to promote soil acidity, poor aeration, and the accumulation of deleterious substances seems obvious, while their depth would favor low soil temperatures. Regarding the relative importance of these different factors, how-

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* See Gates, F. C. Winter as a factor in the xerophily of certain evergreen plants. Bot. Gaz. **57**: 445–489. *f. 1–12.* 1914.

† For references to the literature relating to these various theories, see Dachnowski, Bot. Gaz. **52**: 1–3. 1911.

ever, no definite statement can yet be made, although it seems more than likely that the observed conditions may result from a combination of several causes. Whatever the direct cause or causes, the prevailing consensus of opinion among ecologists seems to be that their ultimate effect on the plants concerned is such as

FIG. 15. Spruce bog surrounding a small pond, Southington. Marginal fringe of *Chamaedaphne*, with small black spruces and tall shrubs in the rear. On the snow-covered hill in the background can be made out oaks, chestnut, and red cedar.

either to directly hinder absorption, or else to indirectly reduce it by retarding root development.

The Origin of the Northern Flora in Bogs.—While soil conditions satisfactorily account for the phenomenon of bog xerophytism, it is doubtful whether the remarkable assemblage of northern plants found in bogs is to be explained on this basis alone. In considering this problem some years ago, Transeau* arrived at the conclusion that the explanation must be sought in the physiographic history of the areas concerned. According to his con-

* On the geographic distribution and ecological relations of the bog plant societies of North America. Bot. Gaz. 36: 401–420. *f. 1–3.* 1903; also 1906, *loc. cit.*

ception: "Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently disturbed, we find the swamp flora, or mixtures of swamp and bog species." The plausibility of some such explanation for the presence of northern plants in bogs was re-impressed on the writer during the past summer in the course of ecological investigations conducted on Cape Breton Island. There the bog is the common swamp type, and its vegetation seems wholly in harmony with the forests of fir and spruce that clothe the surrounding uplands; the transition from one to the other is gradual; bog vegetation there is much less restricted than here, as is evidenced by the fact that species which in Connecticut are confined to bogs commonly occur there in shallow depressions along streams, while a much larger proportion of bog species grow on the uplands. Yet notwithstanding the marked contrast in the upland vegetation there and here, the resemblance of bog vegetation in the two regions, not only in general aspect but in specific composition, particularly with reference to sedges, ericaceous shrubs, and trees, is remarkable. Here in Connecticut, however, in contrast to the conditions farther north, the bog is a comparatively rare swamp type, and its vegetation seems utterly out of harmony with the deciduous forests of the surrounding uplands; the transition from one to the other is abrupt, while the characteristic northern bog plants for the most part are restricted to bogs.

In the first paper of the present series* the writer suggested the probability that subsequent upon the final retreat of the continental ice sheet, this region for a long time was populated by northern types of vegetation which, having originally been forced southward by the advance of the glaciers, once more migrated northward in the wake of the retreating ice-front. During the time that has elapsed since the recession of the ice, variously estimated at from 20,000 to more than 50,000 years, there undoubtedly has been a gradual readjustment of the climate, and as a result of this, coupled with the invasion of plants from the south and west, our present vegetation has been evolved. In the historical sequence of vegetative formations which have occupied

* Torreya 13: 93. 1913.

the region under discussion during this period, there doubtless have been represented many of the types of vegetation which at the present time are characteristic of regions farther north. Thus the first vegetation to seize upon the freshly exposed land areas may have been quite similar to the tundra formation which today is restricted to the far north. But the dominance of the tundra must have been relatively ephemeral, for except as it may possibly be represented by isolated species of plants, all traces of it have vanished. Following the tundra there presumably was gradually developed a type of vegetation essentially similar to that which today prevails in northern Maine and in the eastern maritime provinces of Canada. Forests of fir and spruce dominated the landscape. At this time, associated perhaps with a moister, cooler climate, the relationship between lowland and upland vegetation must have been quite similar to what it now is farther north. The bog was a common swamp type, and bog plants were by no means confined to bogs. Just how long this condition prevailed is of course largely a matter of speculation. It is perhaps significant, however, that red spruce and fir still persist as upland species in certain localities in northwestern Connecticut, while the southern boundaries of the great fir and spruce forests of Maine are scarcely two hundred miles north of Long Island Sound. From such facts as this it seems probable that within very recent geological time spruce and fir comprised an important element in the forests of this region. When in their northward march the deciduous trees, which at present predominate the forests of the state, commenced to invade this region, they doubtless became established first in the more favorable sites, so that there thus arose a mixture of coniferous and deciduous types of forest. Such conditions actually exist in the north-woods today. In northern Cape Breton Island, for example, forests of beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula lutea*), together with hemlock (*Tsuga canadensis*), almost identical in aspect with virgin forests in northern Connecticut,* occupy the intervales and many other favorable sites; elsewhere fir and spruce predominate. Such a condition may have continued in Connecticut for a very long period. Ultimately, however, perhaps to the accompaniment of

* Described by the writer in Torreya 13: 199–215. 1913.

climatic changes, the more vigorous southern species gained the upper hand, so that spruce and fir have largely been eliminated from this region.

In the present connection the discussion set forth in the preceding paragraph is of course significant only as it bears on the question as to the origin of Connecticut bog vegetation. In the opinion of the writer the answer to this question may be stated somewhat as follows. From the above discussion it seems fairly certain that within very recent geological time the vegetation of this region has been quite like that of northern Cape Breton Island today, i. e., the upland forests included a mixture of broadleaf and coniferous forest types and bog vegetation was common in all swamps. As the conquest of the region by the southern types of vegetation progressed further, the coniferous type was first vanquished on the uplands, since here environmental conditions proved most congenial to the invaders. It was not, perhaps, until these uplands had become pretty completely occupied that the last strongholds of the northern plants—the swamps—were stormed.* The northern vegetation in spring swamps was first to succumb, since soil conditions here proved quite suitable for certain of the southern invaders. Similarly the northern vegetation in most lake swamps was gradually replaced by southern types. But the conquest of some of these lake swamps proved a difficult undertaking, owing to the peculiar soil conditions which have been described in connection with the discussion of bog xerophytism. For to these adverse soil conditions the northern defenders proved singularly well adapted—so well adapted, in fact, that many of these isolated plant communities still survive the siege. A bog, therefore, is to be regarded as a relict swamp type whose vegetation represents vestigial remnants of a more northern type of flora which has been much more widely represented in this region within very recent geological time. It does not, however, seem advisable to assume that "the habitat dates back

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* Here again the contemporaneous condition of the vegetation in northern Cape Breton Island affords an instructive analogy. Four of the most characteristic Connecticut swamp trees, viz., *Acer rubrum*, *Ulmus americana*, *Fraxinus nigra*, and *Betula lutea*, are likewise found there; but they are restricted to the uplands, almost never occurring in swamps. This is the condition which the writer presumes obtained in this state at the period in question.

to Pleistocene times,"* since from a physiographic standpoint it is doubtful if such an assumption is tenable.† In the opinion of the writer the bog habitats at present in existence may be of much more recent origin.

As has been mentioned elsewhere,‡ there is abundant evidence tending to show that this invasion of areas populated by northern bog plants is still going on. At several localities in the state are bogs in which black spruce and coast white cedar occur together, and in every instance the cedar seems unmistakably to be gaining the ascendancy. In Southington is a large, boggy swamp now overgrown with red maple and elm. Scattered about in parts of the swamp, however, are numerous specimens of black spruce, most of which are either dead or dying. Similar relations may be observed elsewhere, and it is of importance to note that wherever

* Transeau, E. N., *loc. cit.*, p. 37.

† One of the objections to this assumption is pointed out by Dr. C. A. Davis in a recent letter to the writer. "It is probably a conservative estimate . . . that the end of the Wisconsin glaciation in Connecticut occurred from 20,000 to 50,000 years ago. If even the lower estimate be taken, and we assume that any given bog started 20,000 years ago and grew at its present rate of development, say with the peat accumulating at the rate of one foot per century, it is obvious that in the two hundred centuries which have elapsed, the physiography of the habitat would be entirely changed, and that we would have no bogs at the present day." He cites the occurrence of a "cassandra bog at sea level on the coast of North Carolina. It is certainly five hundred miles south of the greatest known extent of the Wisconsin drift, and on an area which apparently was below sea level not a very long time ago." He further states as his opinion that "such facts make the theory of glacial influence, except so far as the ice sheet provided favorable topographic conditions for the growth of bogs, practically untenable." Nor does he "believe that we need this explanation, since our present climatic conditions closely approximate those of glacial times. We are probably near enough to the borders of the zone of boreal influences so that our flora is a mixed one, not from influences exerted in the past, but from those of the present day; and the fact that we find on all our peat deposits overlapping northern and southern floras, as is shown by every list of plants made from associations growing in bogs, in a way supports this contention. It seems to me that our chief assumption should be that the northern plants are present in bogs because in such places they find conditions favorable for their development and growth, and that they are displaced only when these conditions become unfavorable. The fact that most of the northern plants of bogs have fruits that are attractive to birds, or else very small light seeds—and we know that migrating birds make bogs a part of their southern migration route—would seem to help account for the occurrence of northern plants which, after they are established, spread rapidly." It will be seen that Dr. Davis is not wholly in accord with the views of the writer, much less so with those of Transeau.

‡ Torreya **13**: 99. 1913.

the spruce is cut off it becomes largely, if not entirely, replaced by red maple. While, therefore, the writer's conception as to the origin of spruce bogs is based entirely on circumstantial evidence, the explanation set forth seems to account in a satisfactory manner for the observed facts.

Occurrence of Spruce Bogs in Connecticut.—So far as the writer has been able to ascertain from his own field work and from inquiry among local botanists, fewer than thirty spruce bogs are known to exist within the state. These are distributed as follows: Salisbury*, Norfolk (3)*, Kent (2), Litchfield*, Suffield (6)*, South Windsor (2), Willington*, East Thompson (2), New Fairfield*, Monroe*, Middlebury (2), Southington (2)*. Bogs containing an admixture of spruce and coast white cedar occur at Bethany*, Plainfield (2)*, Willington and Windham; while spruce grows in a red maple swamp at Southington*.

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* Bogs so marked have been visited by the writer.